SONGS OF HUMPBACK WHALES: THE AUSTRALIAN PERSPECTIVE

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Humpback whale songs have been recorded in Australian waters since 1979, mainly off the east coast and generally these have shown the complex and stereotyped structure associated with Humpback Whale songs observed in other parts of the world. Detailed study of the 1982/83 song off the east coast demonstrated a stereotyped, repeating song and established "rules" that governed the song for that period. These rules are broadly similar to those established for the Northern Hemisphere with differences in detail. The sounds that make up the song are also different. The song has changed progressively with time. In some years this has been gradual, but in 1984 the change was so substantial that the 1985 song bore little resemblance to that for 1982–84, and was relatively unstructured. Studies in Australian waters provide a somewhat different perspective to those of the Northern Hemisphere because of differences in the environment and the access to whales. Whereas most Northern Hemisphere recordings have been obtained on the breeding grounds (with the notable exception of the Bermuda area) we have access to the whales along the migration paths which extend for thousands of kilometres along the east and west coastlines. From our observations, the integrity of the song appears to be maintained over large distances (1500 km) of the migration paths, although the sample size is small. However, songs off the east coast are distinctively different to those off the west coast.□

Humpback Whales, songs, marine acoustics, animal behaviour.

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Humpback Whale songs have been studied extensively for stocks in the Northern Hemisphere. Payne and McVay (1971) first demonstrated the existence of a structured, stereotyped and repeating song from recordings of migrating whales off Bermuda, and Winn, Perkins and Poulter (1971) observed similar songs in the West Indies. The song is repeated for long periods and appears to be stereotyped between singers of the same geographical breeding stock, but different oceans have different songs (Payne,1978; Winn and Winn,1978; Winn et al., 1981). In addition, the songs of any stock gradually change with time (Winn and Winn, 1978; Payne and Payne, 1985). Sounds attributed to Southern Hemisphere Humpback Whales were first recorded in the late 1950's (Kibblewhite et al., 1967), but song analysis has been reported for only one recording (Winn et al., 1981), apart for some preliminary work on the east Australian song (Cato,1984).

With the notable exception of the Bermuda recordings, much of the work in the Northern Hemisphere has been in tropical breeding grounds such as Hawaii and the West Indies, and discussion has often focussed on the significance of the song to breeding activities. In the North Pacific and North Atlantic Oceans, Humpback Whales are more readily accessible on breeding grounds than on the migration paths. The situation is reversed in the Australian region, where migration paths follow coastlines for thousands of kilometres, and breeding grounds are diverse (Chittleborough, 1965; Dawbin, 1966). Recent sightings of humpbacks extend along the entire coastline of eastern Australia (Paterson and Paterson, 1984, 1989; Simmons and Marsh, 1986). Known concentrations of whales are along the migration paths rather than on breeding grounds. This paper discusses songs recorded between 17°40'S and 35°20'S on the east coast and between 19°40'S and 32°S on the west coast. While some results are from breeding grounds, most were obtained on migration routes.

There is some interest in the songs of Southern Hemisphere Humpback Whales. It seems that stocks in the two hemispheres are well segregated because most stocks do not usually cross the equator and because migrations are seasonal and thus six months out of phase. Songs in the two hemispheres may have evolved independently over a considerable period of time.

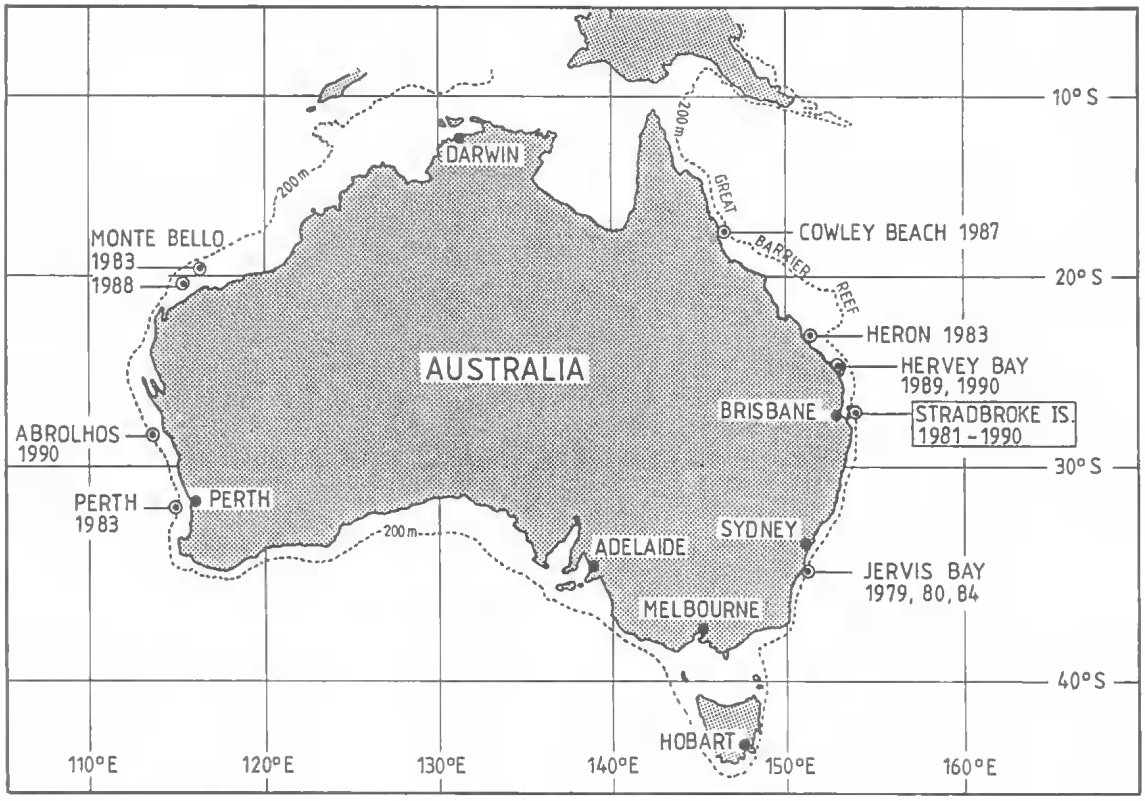

FIG. 1. Map showing the location and year of the song recordings discussed in this paper.

The first Southern Hemisphere recordings of Humpback Whale songs were obtained off New Zealand during 1958–1963 by Kibblewhite, Denham and Barnes (1967). They observed intense activity during April–September, the time of year when most Humpback Whales might be expected in these latitudes (Dawbin, 1966). During 1960–1963 sound activity decreased markedly, coincident with the similarly marked decline in the Humpback Whale population. No analysis of song patterns has been published.

This paper reviews some results of studies of Humpback Whale songs in Australian waters with particular reference to differences in perspective that the Australian region provides, and how these may lead to a better understanding of the song and its purpose.

Samples of songs discussed in this paper are available on compact disc entitled "Songs of the Humpback and Frog Calls of Brisbane and Environs",issued by the Queensland Museum.

METHODS

Data Recording

Sound recordings have been made at a number of locations on migration paths and in breeding grounds along Australian coastlines including those discussed in this paper (Fig. 1). These were single session recordings of a few hours duration, except off Point Lookout, Stradbroke Is. (27°25'S), where data have been recorded on a number of days every year since 1981. Since 1982, recordings have been made off Coffs Harbour (30°18'S) and single session recordings have been made at other locations by an Australian Museum team (W.H. Dawbin, pers. comm.; Dawbin and Eyre, this memoir).

Recordings off Stradbroke Is. were coordinated with the observations of Paterson and Paterson (1984, 1989), and were timed to coincide with the peak of the migration past this point. Recordings have been made during the southern migration in each year (late September,

early October) and during the northern migration (late June, early July) in 1984, 1989, and 1990. Stradbroke Is. is at the most easterly part of the east coast, and this is where the migration paths converge. On the basis of experience during whaling activities in the area, most humpbacks could be expected to pass within 15 km of the shore (Chittleborough, 1965). When this study commenced, this was the largest known concentration of Humpback Whales on the east coast. Even so, long periods of monitoring were required to obtain even a small sample of the song because of the small population at the time (<1/2 the present number;see Paterson and Paterson,1989). As a consequence, sample sizes during the early years of recording were small.

Recordings off Stradbroke Is. were made from a small boat which was allowed to drift in the vicinity of the whale paths off Point Lookout. Whales are in transit at this point, and although they show some meandering, there are only occasional departures from general north or south passage through the area (Cato, 1984). This is an exposed oceanic coast and weather conditions have been unsuitable for recording on about half the days allocated to monitoring.

The recording system consisted of a hydrophone connected via a high pass filter to a low noise preamplifier, and from there to a tape recorder. The preamplifier provided a sufficiently high input impedance to give adequate low frequency response. During recordings, it is desirable to minimise any water flow past the hydrophone, because the pressure fluctuations of the flow, although not acoustic, are detected by the pressure sensitive hydrophone and appear as low frequency noise on the recording. Under some conditions they may be of sufficient level to overload the preamplifier and cause distortion. There is little problem if, as in the absence of wind, the boat and hydrophone drift with the water mass. Usually, however, there is sufficient wind drift to cause some motion of the hydrophone relative to the water. In most cases it was necessary to use the high pass filter to attenuate the low frequencies to avoid overloading the amplifier. Since this filter has a gradual roll off with decreasing frequency, it was possible to correct for its effect in the measurements from tape replay. By experimenting with fairings on the cable, it was found that string wound spirally along the cable substantially reduced the noise from waterflow, presumably by disrupting the shedding of vortices. This was effectively from 1987.

During 1981-1983 the system used was a General Instrument Corporation Z3B hydrophone on 30m of cable, RAN Research Laboratory (RANRL) designed low noise preamplifiers and a Kudelski Nagra III tape recorder. System response was ±3dB from 20Hz to 17kHz, but it was often necessary to use a high pass filter (-6 dB at 55 Hz, –20 dB at 20 Hz) to attenuate low frequency noise from turbulence. From 1984, Clevite CH17 hydrophones and Sony WMD6 or TCD5M cassette recorders were used, giving a system response of 30 Hz–15 kHz, modified by the above filter response when used.

Data Analysis

Sonagrams (spectrograms) were produced using a Kay Elemetrics Corp. Digital Sonagraph and a Spectral Dynamics SD-311 analyser. Spectral measurements were made using a Hewlett-Packard 3582A analyser and Bruel and Kjaer 2112 analyser and 2305 level recorder.

Payne and McVay (1971) defined a "sound unit" as any sound that is continuous to our ears when heard in "real time" (i.e., when replayed at the same tape speed as recorded). These are the individual sounds, or elements of the song. Winn and Winn (1978) used the term "syllable" for a similar purpose. A Humpback Whale song cycle comprises hundreds of sound units but it can be shown that these can be categorised as belonging to one or other of a small number (typically 12-15) different sound types. The term "sound type" is defined here to mean the particular type of sound that a unit belongs to. One sound type is distinguished from another by having different acoustical characteristics. These characteristics can be measured by various methods of analysis, to demonstrate that the sound types are distinctly different. The characteristics of Humpback Whale sounds are such that they are well suited to human aural perception. Thus, with a little experience we can easily distinguish between different sound types by ear. To simplify discussion, descriptive names are used to identify sound types, e.g. "growl", "moan", "whistle". The choice of a name is, of course, subjective but once chosen becomes the definitive name for that particular sound type . It is convenient, in this definition, to allow sound units of a particular sound type to show some variation in character, so long as this variation is small compared with the variation between different sound types. The characteristics of the sound units of a sound type may change with time. If the change exceeds the acceptable variation in the sound

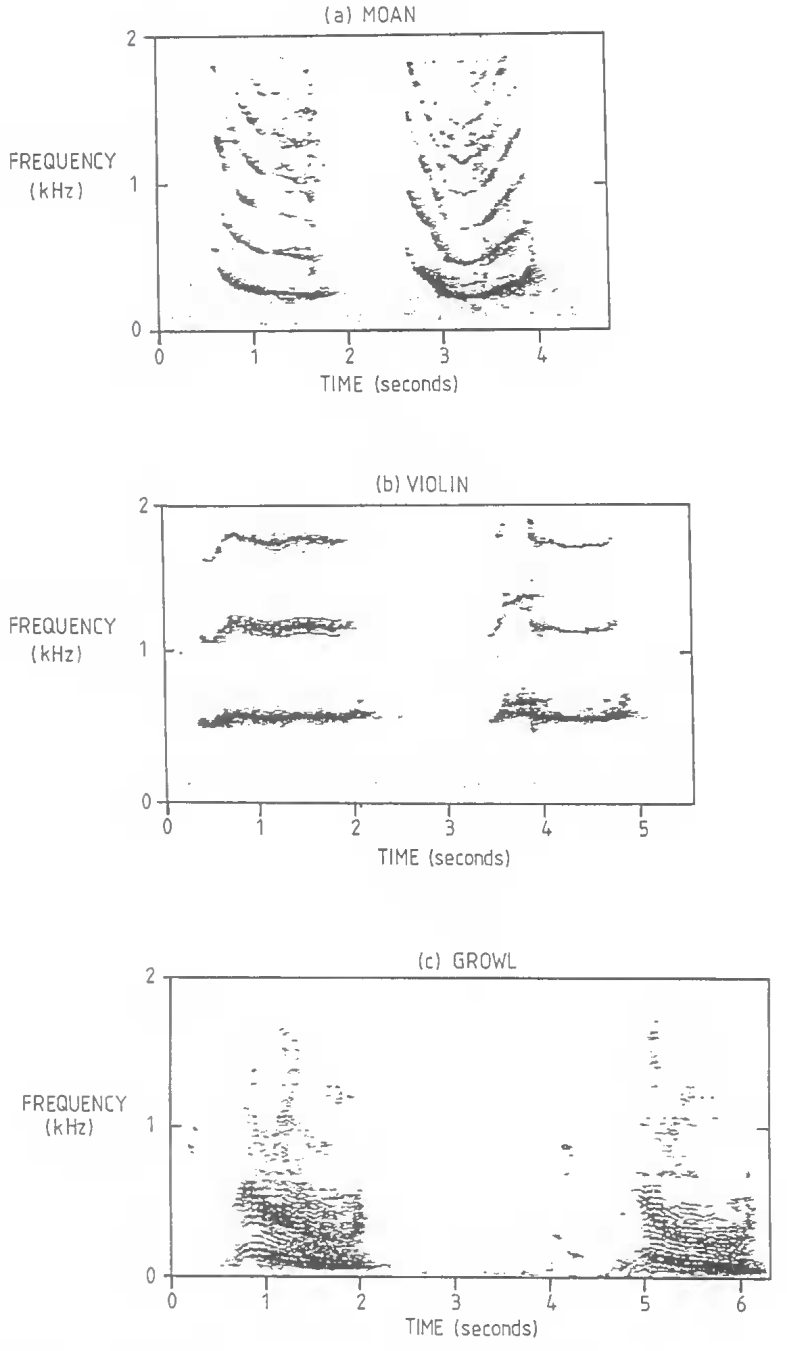

FIG. 2. Sonagrams of two samples of the following sound types: (a) "moan", (b) "violin" and (c) "growl", from theme 5 of the 1983 song off the east coast. The filter bandwidth was 11.3 Hz.

type characteristics, a new sound type must be defined. Sounds type names can be identified with particular years by affixing the year, so that "moan(82)" would apply to 1982 only.

Because sound types are so readily distinguished by the human ear, a major part of the analysis consists of listening to the tapes and noting the sequence of sounds using some shor-

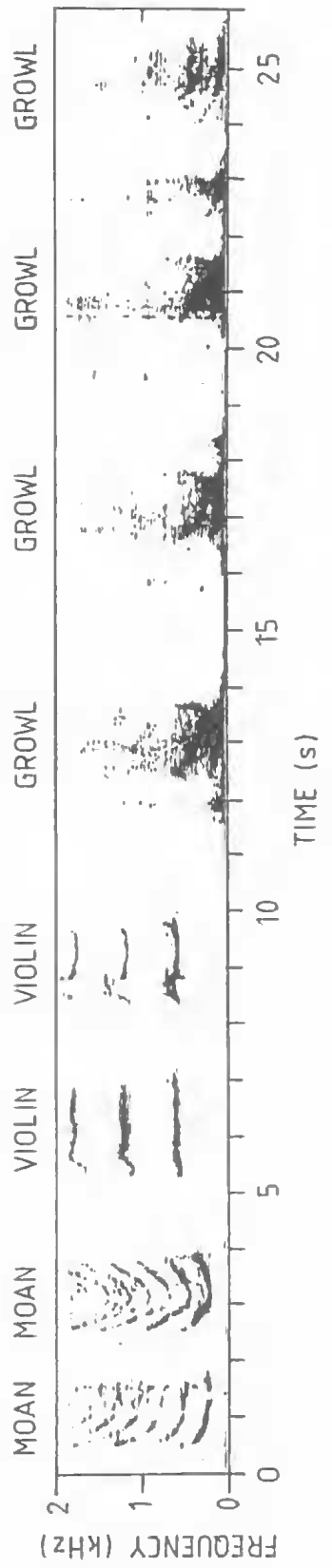

FIG. 3. Sonagram showing how the sound types of Fig. 2 go together to form one complete phrase of theme 5 of the 1983 song off east Australia. The filter bandwidth was 11.3 Hz.

thand notation. From this, the song structure or pattern can be determined. The sounds are also displayed visually as sonagrams which show as a grey scale plot the sound intensity as a function of frequency and time (Figs 2,3). The distinction between sound types and the way they are arranged to form the song pattern can also be determined from sonagrams. The two methods complement each other. Some subtleties detectable by ear are difficult to display or distinguish on spectro-graphic analysis. On the other hand, quantitative comparisons in frequency and time are possible on sonagrams. Sound types can be more readily detectable by aural analysis when the signal to noise ratio is poor (as is the case of distant whale sounds), and a significant proportion of the data can only be analysed effectively by ear. Generally, aural and visual analysis produce consistent results. In the one case we use our aural perception for acoustic analysis and interpretation, in the other we use an instrument to do the analysis and our visual perception for the interpretation. The ear is an effective acoustic analyser, but our aural perception is not equally sensitive to all measurable characteristics of a sound. On the other hand, our instruments have limitations, and their outputs require some assessment, such as the visual interpretation of the sonagram. The sonagram, for example, does not contain all the information in the original sound If we are interested in the importance of the sounds to the whales, we would like to know what characteristics of a sound are detected by the aural perception of a whale. This, of course, is not known. It may be, however, that our aural perception of a sound rather than our visual perception of a sonagram, is closer to the whales' aural perception of the same sound. If we are interested in other aspects of the sounds, such as the mechanism of production, and how they propagate through water, the measurable physical characteristics of the sounds may be more useful than our aural perception.

PROPAGATION OF HUMPBACK WHALE SOUNDS AND THEIR DETECTION AND RECOGNITION

The question of how far Humpback Whale sounds are detectable is of some importance in a study of the song, because it determines the range over which the song can have an effect, whatever its purpose. Unfortunately, because of the nature of sound propagation in water, there is no simple answer to this. Sound is a fairly

localised phenomenon in air because the high absorption attenuation causes the level to fall rapidly with distance from the source. Such attenuation is very much lower in water (at least at the frequencies of Humpback Whale sounds) so that sound levels fall far more gradually with distance. A doubling of distance in typical ocean conditions results in a decrease in level of about 6 dB, whether the doubling is from 100-200m, or from 5–10 km. The detectability depends on the signal to noise ratio at the receiver, that is, the ratio of the whale sound level (the signal) to that of the background noise level. A variation in the signal to noise ratio of 10 db would not be unusual, either through variation in propagation conditions or in the level of the background noise. This corresponds to a variation of a factor of three in detection range. Thus on this basis alone, the uncertainty in estimating the distance to which the sounds are detectable is a factor of three.

The other factors required in this calculation are the source level and the minimum signal to noise ratio for which detection is possible (the detection threshold). Winn et al. (1971) measured broad band source levels of different sounds from the song in the West Indies to range 175–188 dB re 1μPa^2 at 1m. Thompson, Cummings and Ha (1986) measured source levels of non-song sounds of comparable level. Because of the difficulties of identifying singers and measuring their distances during our recordings, we have no estimates of source levels of sounds in Australian waters. We can, however, estimate a lower limit by using the closest possible estimates of the distances of whales during recordings, where this is known. The results support the estimates of Winn et al. Variation in the received level between sound types of the 1982 song recorded from one singer off Stradbroke Is. was about 10 dB. This result and the measurements of Winn et al. indicate that variation in the source level of different sound types from one singer would cause the detection distance to vary by a factor of 3–5. Greater variation would occur if source levels varied between individuals.

Under typical ocean conditions, the distance the sounds would propagate for the levels to fall to that of the average background noise, i.e to give a broadband signal to noise ratio of O dB is about 5.6km for the lowest source levels measured by Winn et al., and 25km for the highest source levels. However, the sounds would actually be detectable at significantly lower signal to noise ratios and thus much greater distances because the acoustical characteristics of the sounds are distinctively different from the background noise. Just how much further the sounds can be detected depends not only on these relative acoustical characteristics, but also on the auditory perception if the receiver is an animal, or on the signal processing gain if the instrumentation is used. A simple experiment in the detection of some Humpback Whale sounds with varying signal to noise ratios by a human subject showed that the threshold of detection occurred at a signal to noise ratio of about -14 dB, corresponding to an increase in detection range of a factor of about five. This was not a rigorous, controlled experiment, and the result should be used only as an indication that detection by a human listener would be at substantially greater distances than the values at which the signal to noise ratio falls to 0 dB. It seems likely that whales are also able to detect the sounds when signal level is less than noise level.

It seems likely, therefore, that Humpback Whales should be able to detect and recognise the song from other individuals for large distances, probably some tens of kilometres, but detection distance will vary significantly under varying conditions, and the actual values cannot be determined without knowledge of the capabilities of the auditory perception of the whales. This may be an important factor in the significance of the song. If the song is detectable for distances of tens of kilometers, behavioural reactions in response to the song may also occur over such distances. The possibility needs to be investigated and the Australian coastlines provide the opportunity for such studies along migration paths.

EARLY RECORDINGS

The first recordings of Humpback Whale sounds in Australian waters were made by Millington and Sneesby off Jervis Bay in October 1979 and in the same area in October 1980. These recordings were obtained incidental to other work and were passed to the author for analysis. In 1979 two whales were observed by aircraft at the time of the recordings (the actual species was not identified). They were estimated to be about 10 km from the hydrophones. There is no direct evidence to indicate that the singer was one of these. However, the recorded sound levels were consistent with a source at that distance, based on the source levels of Winn et al. (1971). Also, given the size of the population in

1979, and the evidence that southward migration paths tend to broaden outwards from the coast well before the latitude of Jervis Bay is reached, it is unlikely (although of course not impossible) that there would have been another whale in audible range. A sample from the 1979 recordings is given on track 1 of the compact disc.

The 1979 recordings are characteristic of an intense, distant source. There is some waxing and waning of the signal consistent with variation in propagation loss and some echoing characteristic of deep water. The background noise was characteristic of the deep ocean, being predominantly from sea surface motion and distant shipping (Cato,1978). As such, it is characteristic of broadband noise – rather featureless, so allowing the distinctive Humpback Whale sounds to be more readily detected than in an environment where a variety of other sounds are present.

The 1979 recordings comprised about four hours of song. Several different sound types were evident and there was evidence of repetition or cycling over periods of minutes, consistent with the Humpback Whale song structure. At the time, identification of the sounds, as due to Humpback Whales, relied on comparison with the extensive knowledge of sounds from other marine animals. The acoustical characteristics of the sounds are such that they are beyond the capability of fish and are indicative of marine mammals. Of the known whale sounds, only those of the right whale have similar acoustical characteristics. However, recordings by the author of sounds of a right whale five weeks earlier (September, 1979) off Wollongong, were different, and showed no evidence of the cyclic and structured characteristics of the sounds recorded off Jervis Bay and typical of the Humpback Whale song. The 1980 recording was about 15 minutes duration, and sound types were generally similar to those of the 1979 recordings. Given the extensive data now available of Humpback Whale sounds off east Australia, there can now be little doubt that the 1979 and 1980 sounds are from humpbacks. Even though the actual sound types are different to any recorded later, their characteristics fall within the same range of variability observed for later recordings.

There are significant and regular gaps in the 1979 and 1980 recordings. This is to be expected for sounds from a distant Humpback Whale. Measurements of source levels of Humpback Whale sounds by Winn et al. (1971) showed a range of 13 dB from the sounds of the highest source levels to those of the lowest source levels. Given a typical propagation loss of 6 dB per distance doubled for deep water, 13 dB propagation loss corresponds to a ratio of propagation distances of four to five. Thus, the higher source level sounds of Winn's data would be detectable at four to five times the distance of the sounds of lower source levels, other things being equal (detectability will also depend on the actual characteristics of the sounds and their relationship to those of the background noise). Although the sounds recorded by Winn et al. (1971) are different to those recorded in Australian waters, it is evident that high source level sound types will be audible at significantly greater distances than those of lower source levels. From song recordings in later years it is apparent that as the signal levels fall relative to the background noise, the lower source level sound types cease to be detected. Gaps in the data appear in a manner similar to those of the 1979 and 1980 recordings.

Since some of the sound types are missing in the 1979 and 1980 data, it has not been possible to make a complete analysis of the song structure. It is clear, however, that the sound types in these songs are unlike those in later recordings off the east coast of Australia, the first of these being off Stradbroke Is. in September, October 1981. This poses the intriguing question: why are the 1981 recordings so different to those of 1979 and 1980? Was there a substantial change in the east Australian song in the 11 months between the 1980 and 1981 recordings, or were the 1979 and 1980 songs alien to this stock?

Since we have never observed alien songs in later recordings, and the 1979 and 1980 songs are very similar, it seems unlikely that they were alien songs, and more likely that the song did undergo a substantial change. We cannot answer this question without further data from that period, but that, of course, is not possible. These songs are now extinct.

The next recordings were obtained off Stradbroke Is. in September, October 1981. Although song data totalled about 65 minutes not all sound types were audible. In July 1982, Dr Dawbin recorded about 20 minutes of song off Cape Byron (pers. comm.).

ESTABLISHMENT OF THE SONG PATTERN AND CHARACTERISTICS

To establish the existence of a repeating stereotyped song, and to determine the rules

governing the pattern for comparison with the songs of the Northern Hemisphere, requires the analysis of many song cycles recorded from a number of individuals. Although there have been recordings of Humpback Whale sounds in Australian waters since 1979, the first data that could be considered adequate for this purpose were not obtained until September, October 1982 off Stradbroke Is. during the south bound migration. This comprised 27 song cycles on 26 September, 7 on 28 September, and 1 on 1 October. Earlier recordings were either too short in duration or not all sound types were detectable.

THEME	SEQUENCE OF SOUND UNITS IN PHRASE		TYPE OF PHRASE
1	6–11	MOAN WHISTLES SIGH	REPEATING
2	3-6	MOAN VIOLINS SIGH	REPEATING
3	2	MOAN VIOLIN SQUEALS SHORT SQUEAL SQUEAL	REPEATING
4	1,2 1,2 4-8	MOANS VIOLINS GULPS	REPEATING
5	2 1,2 3–6	MOANS VIOLINS GROWLS	REPEATING
6	2 Several Several	MOANS SIGH CHUGS,2 SIGHS (repeats) CHAINSAW (repeats) YAPS, CHIRPS (repeats)	EVOLVING

TABLE 1. Basic structure of the Humpback Whale song off east Australia in 1982 and 1983. The sequence proceeds down the table. The phrases of themes 1 to 5 repeat a number of times to form the theme. There is only one phrase of about 20 steps in theme 5.

The song pattern was initially determined from the 4hrs 15mins of data recorded between 0740 and 1240 on 26 September 1982 off Stradbroke Island. Sounds were audible from the time listening commenced until it ceased (because of deteriorating weather conditions) so the period of continuous calling may have extended well beyond 5hrs. In all, 27 song cycles were recognisable, of which 18 were recorded in full. Seven cycles were incomplete because of gaps in recording either due to repositioning the boat or by loss of signal as another boat passed by. The gaps were short enough (equivalent to one to three themes in length) for the continuity of the song to be followed, i.e. the duration of the gap equalled the usual duration of the missing themes. The remaining two cycles were incomplete because of an aberration in the singing. The song jumped from theme 3 of one cycle to theme 2 of the next, with a fragment of theme 6 separating the two, and with no apparent pause in singing. There was an additional gap of 30 min possibly representing 3 cycles of the song, suggesting that there might have been a total of 30 cycles over 5hrs. Song cycle durations (complete) varied from 7 1/2–11 1/2 mins, the average being 9 1/4 mins.

During the period of recording, two groups, each of three whales were observed at distances varying from a few hundred metres to a few kilometres. One group included a calf, however, a comparison of the received signal levels, with the estimates of source level of Winn, Perkins and Poulter (1971), indicated that the other group of three was responsible for the song. For a short period a more distant song was audible.

The general pattern of the song established from these recordings is shown in Table 1. The choice of theme 1 as the start of the song was based on the following criteria, using data from this and later years. On 10 out of the 11 occasions when we heard a whale stop singing at the end of a song session, it has been at theme 6 or the equivalent theme in later years. The eleventh occasion was a rare example in our experience of aberrant singing where themes had been omitted in the two cycles preceding the cycle in which the session stopped (at theme 2). On the one occasion when we observed the start of a song session, it began with theme 1.

Usually the song in 1982 progressed from theme to theme without pause, with the exception of the transition from theme 6 to theme 1 where a pause was sometimes, though not always, observed (data from later years showed a more pronounced pause at this point). Often the sound intensity diminished towards the end of theme 6. On the basis of Northern Hemisphere work, this is indicative of the point in the song

where the whale approaches the surface to breath, and is thus a further criterion of the end of the song. A reduction in intensity is to be expected as a singer approaches the surface because of the interference between the sound waves incident on (striking) the surface and those reflected from it, since they are out of phase. Winn et al. (1971) and Winn and Winn (1978) were able to localise on singers in the West Indies using a directional shipboard sonar, and found that singers came to the surface to breathe at a particular part of the song. Tyack (1981) noted the reduction in sound intensity that occurred at this point of the song and used this as a means of identifying the singer.

It may, however, be misleading to talk of the start and end of a song cycle. Theme 6 could alternatively be viewed as a link between cycles and it is interesting to note that a song session usually stops part way through theme 6 rather than at the end. The structure of theme 6 also differs from that of the other themes.

In structure, the 1982 song broadly follows the rules established for the songs of the Northern Hemisphere. The themes are emitted in the order shown (with rare exceptions) and each comprises a variable number of repetitions of a phrase specific to that theme, except that theme 6 has only one phrase. Phrases comprise a number of sound units in a fixed order separated by gaps of silence which vary from <1/2 sec. to 3 secs. The duration of the sound units varies from 0.1secs for the "whistles" to 4.3 secs for the "chainsaw". There is some variation in the number of repetitions of certain sound types in a theme (Table 1).

Theme 6 differs from the others in that it contains only one long phrase of about 2 mins duration with about 20 steps. Early steps comprise several "chuggs" and terminate with one or two "sighs". Following steps consist of one long sound unit – "chain saw" – rather like the merging of several "chuggs" to form one continuous sound. The final steps consist of several discrete units – the "yaps" – and terminate in "chirps". Themes 1 to 5, on the other hand, contain a number of repetitions (up to 12) of short phrases of 15–25 secs duration each comprising a number (5–13) of sound units.

There are more subtle patterns within the basic pattern (Table 1), and some minor variations. These will be discussed in a later paper. This basic song pattern was generally adhered to in the 40 song cycles from five individuals recorded in September and October 1982. The only exception was the omission of themes in two consecutive cycles out of the 27 recorded on 26 September. Themes 4 and 5 were missing from one cycle, theme 1 from the next. Otherwise, theme order and phrase structure was unchanged.

Songs recorded off Stradbroke Is. in September and October 1983, and off Heron Is. in October 1983 were similar to those recorded a year before with only minor changes. There was so little change in the song pattern, that the structure in Table 1 can be considered to apply equally to both the 1982 and 1983 songs. Some of the sound types showed changes in character but were still clearly recognisable as variants on the 1982 versions.

Sonagrams of samples of three of the sound types from the 1983 song (Fig. 2) have two consecutive samples of each sound type, all from a phrase of theme 5. Note that acoustical characteristics of the sound types are different, but each sound type shows some variation between the two samples, though much less than the difference between sound types. Both "moan" and "violin" are harmonic sounds and would be perceived as having characteristics similar to musical sounds. The fundamental frequency is equal to the interval between the harmonics and this is substantially higher in the case of the "violin", so that it is perceived as having a higher pitch. The frequency (and thus the pitch) is relatively steady in the case of the "violin" but varies significantly over the duration of the "moan", initially falling, then rising. The "growl" has different acoustical characteristics consisting of a rapid succession of broad band pulses.

Figure 3 shows the sound types of Fig. 2 as they occur together to form a phrase of theme 5 (1983).

A sample of the 1983 song commencing with theme 2, is given on track 2 of the compact disc. There are two phrase renditions of theme 2, 6 of theme 3, 1 of theme 4, and 3 of theme 5 in this particular sample. Theme 6, as discussed above, has only one long phrase. The song ends at the "chainsaw" of theme 6 where the whale stopped singing. The sonagrams of Figs 2 and 3 were taken from this particular sample. The recording was made off Point Lookout, Stradbroke Is. on 29 September 1983 in the presence of seven whales (Cato, 1984).

CHANGE IN THE SONG WITH TIME

Over the 12 months from September 1982, the

east coast song changed in the character of some of the sound types and in the song pattern. Not all sound types are audible in the recordings of September 1981 so the pattern for only about 2/3 of the song can be determined. This part of the song is, however, similar in pattern, to the song of 1982, and the audible sound types are similar in character to their 1982 versions.

The song recorded in June, July 1984 (four singers, on separate days) was generally similar to that of 1982/83 in pattern, and changes in the character of the sound types were small. From July to September 1984, however, the song changed substantially. Recordings in early October and November (two singers, on separate days) showed that themes 3 and 5 were much diminished in duration, and the charaeter of the sound types in themes 1, 2 and 6 had changed significantly. By 1985 the changes were so pronouneed that it was difficult to recognise similarities to the 1982/83 song (eight singers, over three days). Themes 3 and 5 were extinct, and many of the sound types of the other themes had changed almost beyond recognition - they had to be considered to be new sound types, even though they may have evolved from the old ones. Themes 1 and 2 became relatively unstructured. Theme 6 now occupied 1/2 the song, partly because of reduction in the earlier themes and expansion of theme 6. The result was a shorter, significantly more poorly structured song than in 1982/83.

Thus, while the song showed a relatively gradual change from late in the singing season of 1981 to early in the season of 1984, the change during the season in 1984 was substantial. By late 1985 song was quite different to that of 1982/83, not only in song pattern and character of the sound types, but also in form of song, being relatively poorly structured. Mednis (this memoir) shows from an analysis of songs recorded off Stradbroke Is. in 1988, that the song later returned to the well structured form of 1982/83.

As discussed above, the sound types observed in the 1979 and 1980 songs off the east coast were different from those of 1981 and later years. The possibility that this was the result of a substantial change in the song in the 12 months from October 1980, thus seems more plausible, in view of the substantial change observed in 1984.

A sample of the 1985 song is given on track 3 of the compact disc. Other singers are audible in the background. This sample is one of the few examples where the last theme (the one that evolved from theme 6 of 1982/83) is repeated, so it is rather longer than most song cycles of 1985.

GEOGRAPHICAL FACTORS IN SONG CHARACTERISTICS AND SINGING BEHAVIOUR

Studies of Humpback Whale songs in the Northern Hemisphere have tended to concentrate on the tropical breeding grounds, with the notable exception of Bermuda (32°20'N). In the north Pacific and North Atlantic, Humpback Whales are most accessible on breeding grounds, because of the congregations in near shore shallow waters such as Hawaii and the islands of the West Indies. Migration paths, on the other hand, tend to be well off shore, and it is only where they approach islands such as Bermuda that there have been significant recordings on the migration paths. Studies to relate song production and behaviour have concentrated on breeding grounds, notably Hawaii (Tyack, 1981, 1983).

The situation is reversed in Australian waters. We have most ready aceess to the whales along the migration paths which follow the thousands of kilometres of the east and west coastlines. Breeding grounds on the east coast appear to be between the Great Barrier Reef and the coast (Paterson and Paterson, 1984, 1989; Simmons and Marsh,1986). On the west coast they appear to lie in the shelf area off northwest Australia. No concentration of whales on either breeding ground has been discovered. As a consequence, most recordings of the song have been from the migration paths, with very little from what could be considered to be breeding grounds (only the two most northerly points on the east coast (Fig. 1) could be considered to be on the breeding grounds). Stradbroke Is. was chosen as the place to record the song when this study commenced in 1981, because this was where a significant concentration of whales were known. More recently, a concentration of humpbacks in Hervey Bay during the southern migration has been established (Bryden et al., 1988).

Humpback whales have been observed along the entire east coast of Australia (10–38°S). The shortest distance by sea between these points while keeping within, say, 50 km of shore is in excess of 3500 km. Humpback whales have also been observed over a large range of latitudes off the west coast (Bannister, 1985; Dawbin and Gill, this memoir). In this study, songs have

been recorded off the east coast at a number of locations between Jervis Bay (35°20'S) and Cowley Beach, near Innisfail (17°40'S). The shortest distance by sea between these two locations is about 2400 km. Off the west coast, recordings have been made between Perth (32°S) and the Monte Bello Islands (19°40'S).

Because the song changes with time, comparisons between recordings from different locations must be confined to recordings that could be considered to be contemporaneous, i.e. separated in time by no more than a few weeks, if any observed differences are to be associated with the differences in position. Recordings off the east coast (Fig.1) were contemporaneous with recordings off Stradbroke Is., with the exception of the 1979 and 1980 recordings off Jervis Bay. In these comparisons, no greater differences could be detected between contemporaneous songs at different locations than between different songs at the same location. The largest separations in these comparisons were Cowley Beach to Stradbroke Is. (1400 km) and Stradbroke Is. to Jervis Bay (970 km).

The first recordings of Humpback Whale songs off the west coast were obtained by a naval vessel in October 1983 off Perth and the Monte Bello Islands, a separation of 1600 km by shortest path. The recordings were separated by only 13 days and comprised one song cycle at the northern location and little more than half the cycle in the southern recording. The part of the song that is common to both recordings is similar. On the other hand these recordings are distinctively different from any recordings off the east coast, including those recorded within a few days off Stradbroke Is. The difference is fundamental: the sound types recorded off the west coast were different in their acoustical characteristics to those off the east coast. Recordings in later years have also shown the difference between the two coasts, for example, the songs recorded near the Monte Bello Islands in 1988 (several song cycles, two singers), and those discussed by Dawbin and Eyre (this memoir).

Although the sample size is small, these results suggest that the Humpback Whale song retains its integrity without geographical variation over a wide range of latitudes along the migration paths of the east coast of Australia.

Humpback whale populations off the east and west coasts of Australia are considered to be separate breeding stocks, with some intermingling in the Antarctic feeding grounds (Chittleborough, 1965; Dawbin, 1966). Evidence from marks recaptured from whales during whaling activities from 1950 to 1962 (Dawbin, 1966) indicates that outside the feeding grounds, the two stocks are well segregated but that a small amount of interchange does sometimes occur. Of whales marked off the east coast, 46 were later captured off the east coast, two off the west coast. Evidence from sightings, catches and catch compositions also indicates that stocks were well segregated, but Chittleborough takes the absence of any statistical differences in morphology as an indication of a small interchange between stocks.

Humpback whale songs in the North Atlantic Ocean differ substantially from those of the North Pacific Ocean (Payne, 1978; Winn and Winn, 1978; Winn et al., 1981). Geographical barriers do not allow the opportunity for interchange between stocks in these oceans as there is south of Australia. On the other hand, similar songs have been observed between breeding grounds which are widely separated by open water at similar latitudes in the same ocean, even though the separation is greater than between the east and west coasts of Australia. The similarities of songs between Hawaii and the Revillagigedo Is., (west of Mexico) in the North Pacific Ocean and between the West Indies and Cape Verde in the North Atlantic Ocean have been reported by Payne and Guinee (1983) and Winn et al. (1981), the separation distances being 5000 km and 4300 km respectively. Using tail fluke photographs to identify individuals, Darling and Jurasz (1983) found one example of interchange between Hawaii and Revillagigedo Is. These results suggest, therefore, that a geographical barrier between breeding grounds or between breeding grounds and a substantial part of the migration route is more important than the separation distance in determining different songs. It might be expected that the geographical separation would need to extend sufficiently far to separate that part of the migration paths over which significant singing occurs. However, a more definite conclusion requires comparisons from other areas, e.g. between east Australia and New Zealand.

TENTATIVE SONG RULES 1982-1985

To facilitate comparisons between hemispheres it is useful to formulate some tentative "rules" which govern the song pattern and sound character off Australia. These "rules" are designed to match as closely as possible the

"rules" of song structure already determined for the Northern Hemisphere and given in the papers cited above. They are thus not necessarily new findings but rather an expression in a way designed to simplify comparison. "Song pattern" is defined as the order in which sound units of the different sound types occur. "Sound character" is defined as the spectral and temporal characteristics of a particular sound type. The definition of "sound type" is given in the section on "Methods" From the analysis the following features of the song have been established :-

(a) The song consists of several themes (six in 1982/83) in a fixed order, each comprising a variable number of renditions of a phrase which is specific to that theme.

(b) Each phrase consists of several discrete sounds (syllables or units) in a fixed order separated by short periods of silence (typically 0.5-4secs).

(c) Each sound unit is a sample of one or other of a small number of basic sound types (12 in 1982/83) appropriate to that particular song. These are distinguished by their temporal and spectral characteristics (referred to as 'character' in this paper).

(d) The song pattern and the sound character at any time appear to be maintained by individuals of a stock for great distances along the migration paths and breeding grounds, although the sample size is small.

(e) The songs are distinctively different between stocks on the east and west coasts.

(f) Both song pattern and character of the sound types change progressively with time.

(h) Songs heard simultaneously appear to be independent and unsynchronised.

DISCUSSION AND CONCLUSIONS

Humpback whale songs recorded in Australian waters show a structure that is basically similar to that of the Northern Hemisphere songs. Although a song may contain some hundreds of sound units, all belong to one or other of a small number of sound types (12 in the 1982/83 song off east Australia). The song changes with time at a non uniform rate. Off east Australia the rate of change was gradual in 1982 and 1983, but a substantial change during the singing season in 1984 led to a substantially different song in 1985. This song was unusual in being poorly structured compared to the earlier songs.

There are more subtle patterns in the song than have been addressed in this paper. There are also small variations in pattern and in the characteristics of the sound types that warrant more detailed analysis. Information theory indicates that a signal can carry information only to the extent that it is unpredictable. Thus in a generally stereotyped song, it is the variation from the stereotype that has the potential to carry information.

Songs are distinctively different between the east and west coasts of Australia. It seems that a geographical barrier between stocks where most of the singing occurs, i.e. on the migration paths and breeding grounds may be enough to ensure that songs are unrelated, even though the stocks may intermingle in the feeding grounds.

In the samples available, the song appears to maintain its integrity over the very wide range of latitudes over which singing occurs off the east coast. This leads to a number of interesting questions. How are changes in the song communicated along the coast, and at what rate? Do the changes originate at any point where singing occurs or are there preferential source regions? At what distance from a singer does the song affect the behaviour of other whales?

The Australian coastlines provide access to Humpback Whales for thousands of kilometres along the migration paths and into the breeding grounds. The breeding grounds appear to be diverse and there may be no clear demarcation between these and the migration paths. Although whales appear in Hervey Bay as they migrate south, their behaviour shows a greater proportion of activity of the type associated with the breeding grounds than is observed further south off Stradbroke Is. These conditions provide the opportunity to study the relative significance of the song in breeding and migration. Does the proportion of whales singing and related behavioural reactions vary along the coastline? The population of Humpback Whales off the east coast has more than doubled since the early recordings were made (Paterson and Paterson,1989) and there are now more people making recordings, so that we now have prospects for obtaining much larger data samples than were available for the analysis on which this paper was based. There are good prospects for progress in understanding the significance of the song in migration and breeding.

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